THE WEST AUSTRALIAN PITCHER PLANT (*CEPHALOTUS FOLLICULARIS*), AND ITS PHYSIOLOGY.

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The pitcher plant of Western Australia is noteworthy as one of the most characteristic endemic plants of one of the most interesting floral areas of Australia. It is the only species of the genus Cephalotus—a genus confined to a small area in south-west Australia. In addition to this, however, it is the only representative of the Cephalotaceæ, an order which does not seem to be closely related to Nepenthes or Sarracenia, although the pitchers are remarkably similar in these different genera. The area in which this plant is found is apparently usually considered smaller than it really is, for one generally hears that Cephalotus is only found near King George's Sound. As a matter of fact it extends westwards probably at least as far as Deep River, and although its range has not been followed to the east it is believed that Labillardiere's specimens came from Esperance Bay. Labillardiere's collections were made in connection with the Expedition of D'Entrecasteaux; the two vessels "La Recherche" and "L'Esperance" visiting the south coast of Western Australia towards the end of 1792.

Whether the plant originated in Western Australia, or is now confined to a tiny fraction of a former larger area, is a question that cannot be discussed in the light of our present knowledge.

Cephalotus is found on swampy land round Albany, growing on peaty soil which is wet in summer and quite sodden in the long wet winter of this region. It is associated in places with the interesting Lycopod—*Phylloglossum drummondii*. The plants are low and quite inconspicuous amongst the reeds—the photographs (Figs. 1, 2, and 3) indicate the usual type of situation. The flower stalks, which grow up in the early months of the year and have a transitory existence, are by far the tallest parts of the plant. Indeed they may reach a height of two or three feet (10-20 centimetres is the height given by Diels & Pritzel, but I am informed that this is unusually low). The flowering period extends between January and March.

Under natural conditions two kinds of leaves are developed, forming a rosette round the stem (at least this is the case in plants growing on the more open ground). The pitchers are modified leaves situated more externally, whilst the ordinary leaves are placed more to the centre. These leaves do not seem so abundant in nature as on our plants grown in the laboratory at Perth, and at the time of correcting proofs of this paper (12th August) all the pitchers have died and withered, whilst the ordinary unmodified leaves appear green and fresh.

Fig. 1.
General view of vegetation where pitcher plants grow, near Albany, W.A.

Fig. 2.
Pitcher plants on ground amongst grasses, etc.

It will be unnecessary to enter into a closely detailed description of the plant here—a very good account may be found in the Proc. Linn. Soc. N.S.W. for 1904 (Hamilton). The full-grown pitchers are about 1-1½ inches in depth, but in many places smaller specimens are the rule. The stalk is attached to the back of the pitcher just below the hinge of the lid. A well-developed flange runs down the front of the pitcher in the middle line, and this bears long stiff hairs. To the right and left of this flange a wing runs from the pitcher rim laterally until it finally merges into the general surface. These wings, like the median flange, also bear stiff white hairs. The very young pitcher, whilst it is only a small swollen body at the end of a long stalk, presents a rather curious appearance owing to the presence of the hairs referred to above. They are relatively so long compared with the size of the young pitcher and so numerous that the young leaf literally bristles with them. The effect is clearly seen in the photograph (Figure 4). The young pitchers are bright green in colour, but as they become older they develop tints of crimson and purple. It is noteworthy that these colours have not been assumed to any extent by our laboratory plants. This may have been due to the lack of insect nutrition (the pitchers have developed and the plants have been grown now for 27 months without insect food), or it may have been the result of other artificial conditions. Further experiments may indicate the factors responsible for the change in tint assumed by the large pitchers in the field. Hamilton states his belief that the ordinary leaves develop in autumn, reach their full maturity in spring, and then gradually go off, whilst the pitchers grow in winter and spring and are fully formed and functional in summer. We have found that the pitchers are apparently functional throughout the year, although much more so in summer; and, so far as our pot plants are concerned, the greatest development of pitchers has taken place in March-April.* This might possibly be a change due to artificial conditions, although it is unlikely, since the plants are being grown in their native soil.

Now, although Cephalotus is not closely related to Nepenthes and is far removed geographically from the home of the latter, there is a remarkable resemblance between the pitchers of these two plants. The same inverted lip is present with the ribs and grooves, and a lid serves the purpose of keeping out rain but is not capable of movement after once opening. Furthermore, on the outer surface of the pitchers we have in both cases a development of lateral wings. On the other hand, there are important differences —the histology of the glands is not the same, and there are morphological divergences. We might regard the pitchers of these two genera, Nepenthes and Cephalotus, as instances of convergent evolu-

* This has now taken place for the second successive year on a plant grown for 27 months in the laboratory.

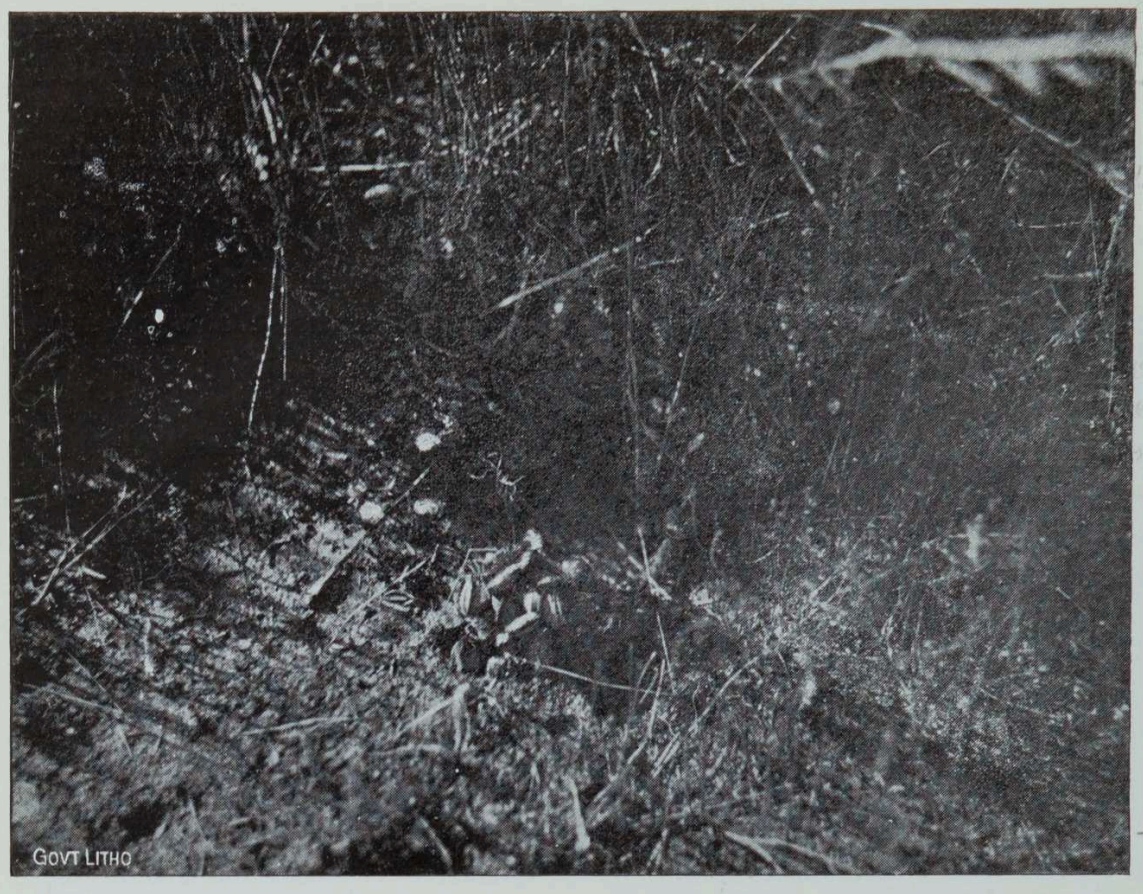

Fig. 3.
Pitcher plants on ground (nearer view).

Fig. 4.
Pitcher plants, young and old specimens.

tion—a similar direction having been taken in the evolution of two morphologically similar structures.

This should accentuate our interest in the study of the chemistry of the two forms.

The Epidermis of the Pitcher.

The inner surface of the Cephalotus pitcher is quite smooth and glossy below the rim. This surface is highly glandular. It extends from the incurved lip down to two lateral kidney-shaped areas, which are very conspicuous (Fig. 5, Lat. p.a.). Each area is raised above the general surface and deeply pigmented. These dark-coloured lateral patches have been named the Lateral Gland Areas. We shall see that this nomenclature is not altogether satisfactory—in fact one may say it is incorrect. With a hand lens, or even the naked eye, it is possible to see small projections along the upper portion of each lateral area. At first sight it might be thought that these were characteristic features of the lateral areas. Such is not the case, although it has been believed that they were. Closer examination reveals the fact that these projections are glands and that they occur over a large area of the surface of the pitcher, although they vary in size and are smaller but more numerous elsewhere. The illustration (Fig. 5) which represents a pitcher cut

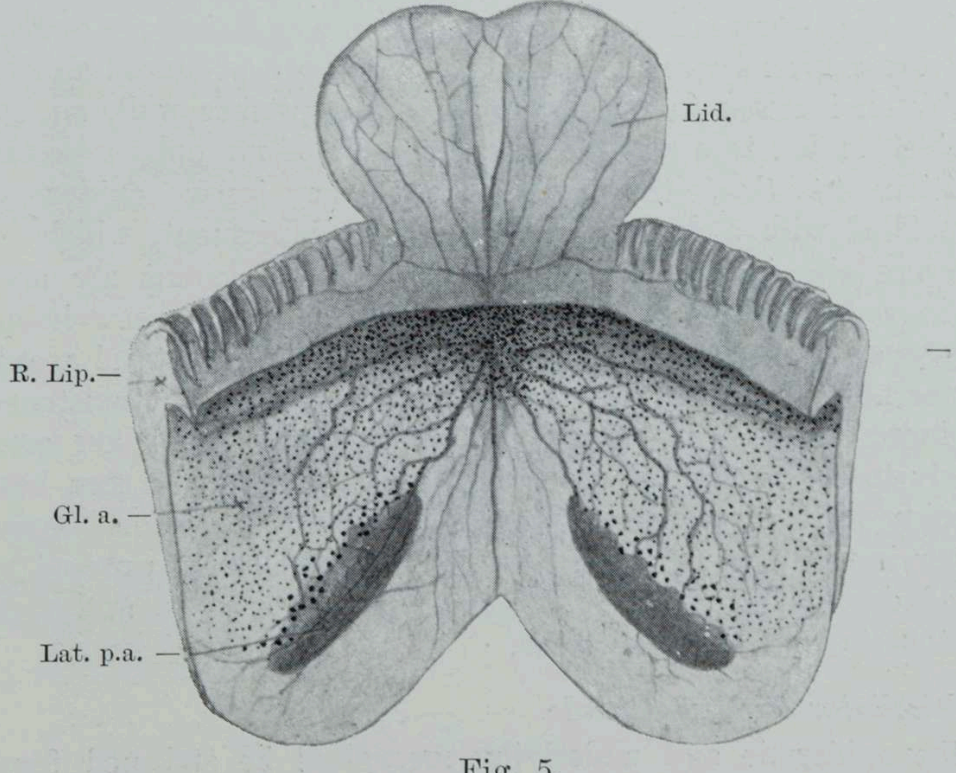

Fig. 5.
Pitcher cut down front and folded to right and left, to show view of internal surface.
Gl. a.—Glandular area ; Lat. p.a.—Lateral pigmented area ; Lid.—Lid ; R. Lip.—Lip of Pitcher.

down the front, the two sides being folded back, illustrates very clearly the distribution of the glands. It will be seen that they are most numerous and smallest just below the incurved lip and in the

region where the vascular bundles from the pitcher stalk enter the pitcher wall. The most obvious and largest glands border the lateral areas but do not extend far upon them (see Fig. 6).

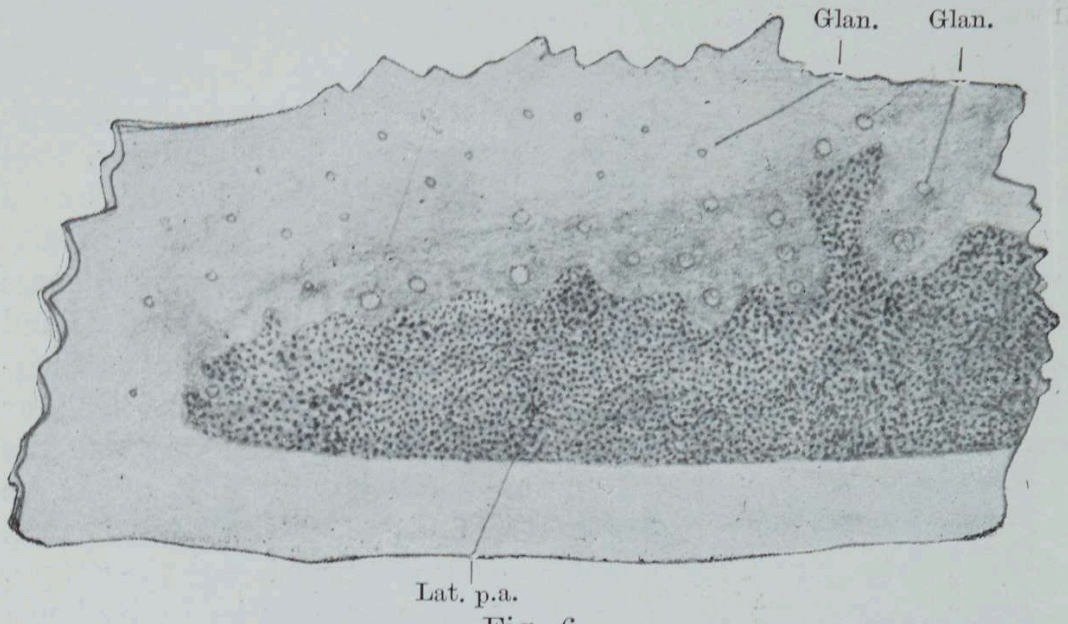

Fig. 6.

View of internal surface of pitcher about the lateral pigmented area.

Glan.—Large glands ; Lat. p.a.—Lateral pigmented area.

Microtome sections through the lateral areas show at once that the very distinct demarcation of these regions is not due to the aggregation of these special glands. The lateral areas are produced almost entirely by an increase in the thickness of the pitcher wall, an increase which is due to a stronger development of mesophyll tissue. In addition to this, the cells below the inner epidermal layer are filled with a dense and deep-coloured pigment, which in places occurs also in the epidermis itself. Starch grains are also present in some of the cells. There is, however, a remarkable feature present in connection with the epidermis of the lateral areas, a character now discovered for the first time. This is the existence of very large numbers of extraordinary "stomata." They are confined solely to the surface of the lateral areas, and can be seen best by stripping off the epidermis (Fig. 10). Below the lateral areas the pitcher is free from glands (Fig. 5). We shall now proceed to a detailed description first, of the multicellular glands, and then of the stomata and stomata areas.

The Multicellular Pitcher Glands.

If the epidermis and underlying mesophyll be stripped from the interior of the pitcher and examined in surface view, the difference in the size of the glands is at once obvious. The appearance presented is illustrated in Figs. 7 and 8. Fig. 7 represents one of the small glands from the surface near the lip of the pitcher. Fig. 8 is one of the large glands from the upper margin of the

lateral pigmented area (Fig. 6, Glan.). No stomata are to be seen in connection with these glands, and there is no sign of any opening. The epidermis is raised very slightly where the gland interrupts its continuity.

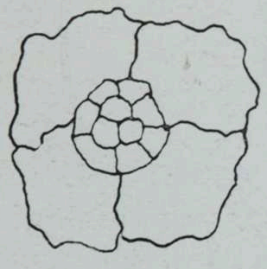

Fig. 7.
Surface view of gland from interior of pitcher near lip (magnified).

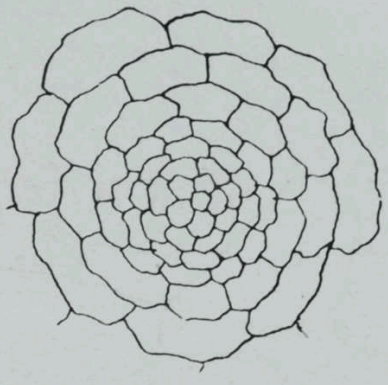

Fig. 8.
Surface view of gland from interior of pitcher near lateral pigmented area (magnified).

In section each gland is seen to be a more or less spherical mass of cells covered over by the epidermis except at one point (a little circular area when observed in surface view). At this point a few of the gland cells reach the surface. No depression or cavity is present into which secretion is poured, nor is any other opening into the gland present. The secretion must pass from cell to cell through the thin walls until the surface is reached and the exudation flows down the walls of the pitcher cavity.

The gland cells contain protoplasm, which is always free from the pigment found in the adjoining cells.

The glands are in close relation with the vascular bundles, and a rich development of spirally thickened tracheids indicates that a good water supply is ensured. On the whole the glands bear a striking resemblance to Hydathodes—the hydathodes of the leaves of *Plumago lapathifolia* for example.

We shall be quite safe in considering these glands as responsible for the secretion of the liquid in the pitchers, for their position prohibits their use as absorbing organs—a large part of the area bearing them is often above the level of the fluid in the pitcher. It remains to be seen whether the specialised lateral regions have any secretory function.

The Stomata of the lateral pigmented areas.

Hamilton states "that the epidermis of the lateral areas is composed of crenate cells in all respects like those of the preceding region" (the inner wall of the pitcher). He misses the significance of the stomata, and only mentions that "at the anterior point of the gland mass where it runs into the ordinary surface there occur some cells which are very puzzling. They are remarkably like stomatas, but there is not always an opening between the guard

cells." Hamilton evidently did not obtain sections of them, and did not observe that the whole surface of the lateral pigmented

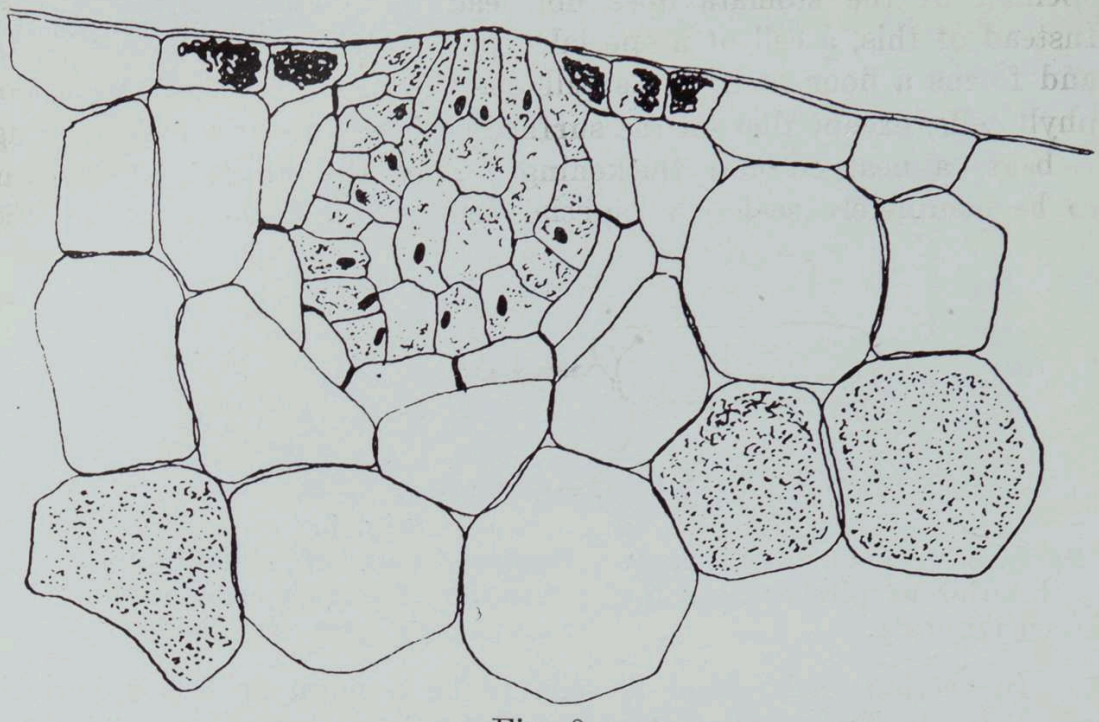

Fig. 9.
Transverse section of pitcher through a large gland.

areas is covered with these structures. Looked at from above, the aperture of the stomata is large compared with the width of the guard cells, and is always almost circular in outline. There is no evidence to show that this shape ever changes. In other words, the aperture between the guard cells is permanently open (see Fig. 10). Sections are required to elucidate the structure, and they are not

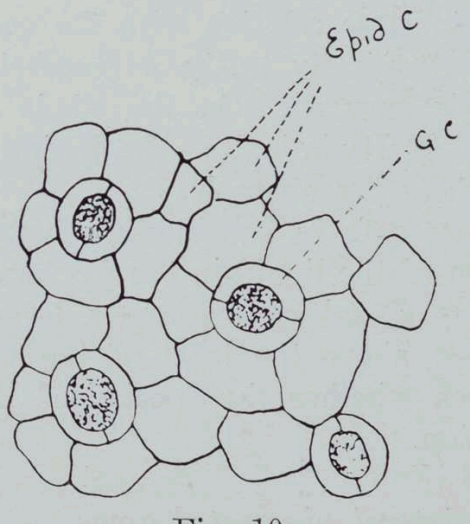

Fig. 10.
Epidermis removed from lateral pigmented area.
Epid. C. = Epidermal cells. G.c. = guard cells.

easy to obtain—hand sections being quite out of the question. In paraffin sections the guard cells are observed to be quite small in relation to the aperture of the stomata and the other epidermal

cells (see Fig. 11). The most striking feature, however, is that the opening of the stomata does not lead to a sub-epidermal space. Instead of this, a cell of a special type lies below the whole stomata and forms a floor to it. This cell has the usual form of the mesophyll cells, except that on the surface covering the stomatal opening it bears a neat circular thickening. Thus the stomata all appear to be completely sealed by special cells. We shall call these the

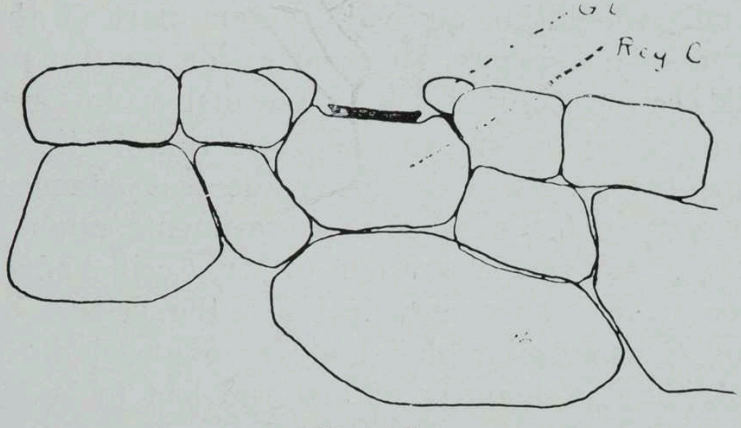

Fig. 11.
Transverse section through lateral pigmented area, through one of the stomata and regulating cells.
G.c. = guard cell. Reg. c. = regulating cell

Regulating Cells (Fig. 11, Reg. C). It must be emphasised that the thickened area on these cells is most definite and sharply marked, and this, in fact, led us to conclude that it was not a mere thickening to occlude the stomata permanently. It will be observed (see Fig. 11) that if the regulating cell is not turgid the thickened area does not touch the guard cells and there is a thin walled area left all round. We conclude from this that the regulation of the stomata opening is carried out, not by changes in the guard cells, but by the movements of the outer wall of the regulating cell. If the pad is forced out by the turgidity of the cell it shuts up the aperture. There are no glands associated with these stomata, and from their specialised structure and localised distribution it may be assumed that they are the absorbing organs of the pitcher. Thus the lateral pigmented areas should be termed the Lateral Absorbing Areas rather than the Lateral Gland Areas.

Further microchemical studies will be necessary before many of the curious features of the Cephalotus pitchers are understood. It becomes, however, more and more evident that the physiology of these pitcher plants is not so simple and easily explained as some botanists have imagined.

The Physiology of the pitchers of Cephalotus Follicularis.

From the year 1874 onwards there has been no inconsiderable discussion amongst botanists on the question of the digestive powers of certain secretions produced by the insectivorous plants. The pitcher plants of the genus Nepenthes have stimulated most of this

discussion, the results of experiments often lending themselves to various interpretations. The West Australian pitcher plant, owing to its more limited range and the absence of trained biologists in Western Australia, has been merely referred to from time to time, suggestions only being put forward. Yet experimental work on this plant offers more of interest than new researches on Nepenthes, inasmuch as it should be interesting to see whether an Australian plant which has evolved on parallel lines to another genus of a different family inhabiting quite a different part of the world, has evolved a similar physiology. In other words, has the parallel evolution in form been accompanied by a parallel evolution in function? It has been my good fortune to visit from time to time the districts where Cephalotus grows, and during the last summer vacation I was able to carry out a number of experiments upon the secretion of the pitchers. My thanks are due to Mr. Cecil Andrews, Director of Education, who kindly arranged for the science room in the Albany State School to be placed at my disposal during the holidays. A considerable quantity of material had to be brought from the University Laboratories, Perth, and the Department of Chemistry aided me considerably in making up certain of the reagents used.

It is well known that the nutrition of typical green plants is autotrophic—the plant by virtue of the pigment termed chlorophyll and the energy of the sunlight is able to build up its food from simple inorganic substances. Carbon is obtained from the carbon-di-oxide of the air, and nitrogen, except in a few cases, is procured from nitrates present in the soil. Certain examples are known where, owing to an imperfectly developed chlorophyll apparatus, a portion of the organic food is taken from the environment, and there is a class of plants the members of which are unable to assimilate carbon-di-oxide at all and consequently depend entirely upon organic materials. These are known as heterotrophic plants, the fungi being excellent examples. But all the insectivorous plants we have named possess leaves and chlorophyll and have normal roots. At first sight, therefore, the possession of an elaborate apparatus for the capture and ingestion of organic matter seems quite uncalled for. This feature is rendered still more mysterious by the fact that many of these plants have been cultivated in laboratories and grown over long periods without the provision of insects or other organic matter. Darwin cultivated Droseras, and we have had specimens of Cephalotus for twenty-seven months, during which time new leaves have developed and numerous new pitchers have been formed—the plants also flowered in the laboratory. No insects were utilised by the plant at any time during this period.

In specimens of Cephalotus obtained from Albany the pitchers were, with few exceptions (and these were newly opened pitchers),

full of insect remains; the insects most common being ants, flies, and beetles. Other insect groups were represented and more odd specimens were occasionally found, such as fly larvæ, frog spawn, and snails.

The pitchers of Nepenthes are found similarly loaded, even small birds being sometimes captured by the plant. This, however, is an accident, the birds being either after the water or the captured insects.

The first observations of the digestive power of the Nepenthes pitchers were made by the famous botanist Sir Joseph Hooker, and the results were made public at the 1874 meeting of the British Association at Belfast. Hooker found that "after twenty-four hours' immersion the edges of cubes of white of eggs were eaten away and the surfaces gelatinised, fragments of meat were rapidly reduced, and pieces of fibrin weighing several grains dissolved and totally disappeared in two or three days." It is noteworthy, however, that even at this stage Hooker did not jump to the conclusion that the digestion was wholly due to the liquid secreted by the glands of the pitcher, although he does not definitely state what other agency he had in view. Hooker's results stimulated inquiry, and in 1875 Lawson Tait stated that he had abstracted a substance closely resembling pepsin from the pitcher plant liquid. The next year, 1876, brought further information, Gorup-Besanez announcing that the liquid from the pitchers was neutral or acid according as to whether the pitchers were unstimulated or stimulated, and that, whilst the acid fluid digested fibrin within two hours at 20 C., the neutral liquid had no effect even after 24 hours. This worker demonstrated also the presence of peptone (a product of the peptic digestion of proteids) at the end of his experiments. In 1877 Vines, who had conducted a most careful series of experiments on Nepenthes, published the first paper on his investigations. He agreed with the previous workers that the fluid secreted by the pitchers contained a digestive ferment or enzyme which, like the pepsin of the human stomach, acted upon proteid in a slightly acid medium. These views were held for a few years until in 1890 Dubois, experimenting with fluid from various species of Nepenthes, came to a different conclusion. This investigator stated that if the fluid was taken from closed pitchers by means of a sterilised pipette it had no action on cubes of egg albumen even at temperatures between 35° and 40°C. He then examined the open pitchers and, as a result, stated that the disintegration of proteids was due, not to a digestive enzyme, but to the action of bacteria. He concluded that Nepenthes was not really a carnivorous plant and that the obvious digestion was only a false digestion. The same point of view was taken by a Russian scientist (Tischutkin) in 1892. The opposition brought forward further discussion and the next worker,

Goebel, returned to the point of view taken up by Hooker and Vines. Vines took up the subject again and conducted further researches in 1897 along lines which precluded the action of bacteria. As a result of this work our knowledge of the Nepenthes pitcher fluid stands somewhat as follows:—

1. Digestion of fibrin and other proteids takes place if the pitcher fluids are acidulated—even if substances such as prussic acid are present which prevent the action of bacteria.
2. The pitcher fluid varies from neutral to distinctly acid, but that of open pitchers in which insects are present is as often neutral as acid.
3. Only a minute quantity of proteid is present in the pitcher fluid.
4. The products of digestion are not true peptones, and further investigations are required.

Now let us turn to Cephalotus. In Pfeffer's "Physiology of Plants" the following statement is made which concerns Cephalotus:—

"In the pitchers of Sarracenia, Darlingtonia, Cephalotus, and probably also in the bladders of Utricularia, *no* enzyme is secreted, but nevertheless nitrogenous products set free by bacterial decomposition may be absorbed."

Nepenthes is put in a different category from Cephalotus. Geddes states:—"The recent researches of Professor Vines (1897), although ascribing the digestive powers of Nepenthes to a true proteolytic ferment in the presence of an acid, yet agree with those of Professor Dubois in regarding all other cases of so-called digestion amongst pitcher plants, with the possible exception of that of Cephalotus, as due to putrefaction set up by the microbes always present in the pitcher fluid." We have here a statement which sums up pretty well the present position with regard to Cephalotus—a position of uncertainty which is not based upon any experimental work whatever.

During the month of September last year work was commenced on pitcher plants at Albany. In the first experiments the fluid was removed from the pitcher by a sterile pipette, and brought back in sterile tubes to the laboratory. Fibrin was chosen as the proteid for digestion, and fresh fibrin was obtained through the aid of the Perth Public Health Department. It is removed from sheep's blood by whipping. Test tubes were set up containing—

1. Fluid from pitchers + fibrin.
2. „ „ + fibrin + antiseptic.

Several experiments of this kind were carried out, but in all cases no alteration of the fibrin took place even after several days. An-

other series of experiments were then set going in which marked pitcher plants in the swamps were fed with pieces of fibrin. These plants were visited at frequent intervals and the condition of the fibrin in the pitchers examined, as also the composition of the contained fluid. The results were negative—no digestion taking place nor any alteration, except in one case, where putrefaction had resulted in the breaking down of the fibrin. As putrefaction is not found in the pitchers full of insect remains, and as it was exceptional here, this solitary case was not considered of much importance. Finally a number of pitchers were chopped up and extracts made with water and glycerine. These extracts were used for the digestion of fibrin. The results so far as naked eye observations were concerned were again negative, and chemical tests were rendered practically impossible with the means at my disposal owing to the colour changes in the pigment which came out in the extracts. This first inquiry, which was carried out rather empirically, only stimulated my interest, so that a laboratory was fitted up in the summer and the question was tackled with a better equipment for carrying out the work.

Pitcher plant fluid was obtained with the same precautions as before from plants living about a mile from Albany. The solution which usually contained a considerable quantity of insect bodies was brought straight back to the laboratory and filtered. The fluid was usually quite neutral to litmus, but there was a tendency to show a slight acidity when phenol phthalein was used as an indicator. Four tubes each containing 2ccs. of pitcher plant fluid were set up.

Tube No. 1 contained fibrin and pitcher fluid alone.

Tube No. 2 contained fibrin and pitcher fluid and 1 drop HCN.

Tube No. 3 contained fibrin and pitcher fluid and 0·1 CC. Decinor. HCl. and 1 drop HCN.

Tube No. 4 contained fibrin and pitcher fluid and 0·2 CC. Deci. HCl. and HCN.

The experiment was set going at 4 p.m. Thursday.

On Friday morning, 9.30 a.m., no digestion had taken place in Nos. 1 and 2, but in No. 3 the fibrin was digested, and in No. 4 it was partly digested. This was the first indication of digestion taking place. The two first tubes were left standing and by Sunday digestion had also taken place in tube No. 1, but *not* in No. 2. The difference between these two tubes was that No. 1 contained no HCN., and since the smell of putrefaction was well apparent there the results of the experiment can be easily explained.

Digestion of the fibrin had only taken place in the acidulated pitcher fluid, but it had taken place there despite the action of an antiseptic which prevented the growth of bacteria. In the absence of both acid and antiseptic, putrefaction had taken place whilst

in the presence of HCN, but no acid whenever there was no digestion. These experiments were repeated with controls and extended. Tubes containing fibrin and pitcher fluid, but with neither acid nor HCN, were repeatedly set going. The results were always the same, putrefaction took place due to bacterial action and the fibrin was broken down. This action, however, took some time and usually no change was observed during the first day or two. The absence of this reaction in the experiments carried out in the winter is to be explained by the low temperature in the unheated room used as a laboratory.

It will be noticed that the pitcher fluid which had been acidulated broke down the fibrin and brought it into solution very rapidly indeed—much more rapidly than when bacteriological action was allowed to take place alone. Controls showed that a proper care in the addition of HCN effectively prevented bacterial action whilst treatment of fibrin with acid and HCN alone in another set of control experiments enabled us to determine exactly what was due to the pitcher fluid.

Starch solution was apparently left unchanged, at all events the starch to a large extent remained and there was no difference in the colour reactions between tubes with pitcher fluid and control tubes with plain water.

Amongst the series of tests the following may be mentioned as an example:—

Tube 1—Fibrin + 5CC. Pitcher Fluid + HCN. No acid.
Tube 2—Fibrin + 5CC. Pitcher Fluid + HCN + 0·2 CC. N/10 HCl.
Tube 3—Fibrin + 5CC. Pitcher Fluid + HCN. + N/10 Alkali.
Tube 4—Fibrin + Water + HCN + 0·2CC N/10 HCl.
Tube 5—Fibrin + Water and HCN. No acid.

Tubes 4 and 5 were controls to determine the effect of the N/10 HCl upon the fibrin. The results were as follows:—

1. No digestion took place.
2. Digestion of the fibrin in a few hours.
3. No digestion.
4. No digestion but fibrin cleared and swollen.
5. No digestion.

It will be seen that the acid alone was incapable of bringing about the results observed in the tubes to which pitcher fluid and acid had been added. Thus in the fluid from the Cephalotus pitchers there is ample evidence of the presence of a substance which readily digests proteid in the presence of small quantities of acid. This is the first record of such for the pitcher plant of West Australia.

Another point to be made, which is equally interesting, is that the conditions under which we have observed digestion taking place

are practically identical with those discovered by Vines to apply to Nepenthes.

Now Vines concluded in the case of Nepenthes that digestion, as we have seen it taking place (in acid media *in vitro*), was proof of the function and mode of function of the pitcher secretion. It seems likely that this conclusion is somewhat premature. The fact that in an acidulated medium in a glass tube digestion takes place does *not* prove that the same takes place alone, if at all, in the pitchers of the plant, especially since no certain digestion can be observed in the absence of acid. The pitcher fluid was taken from stimulated pitchers, *i.e.*, pitchers containing numbers of insects, consequently it would be natural to suppose that the fluid would digest without the addition of acid. This does not appear, however, to be the case in *vitro*. We might therefore even go so far as to say that the presence of a true digestive ferment in the pitcher fluid was an accident and that it was not used normally by the plant. Whether such a statement be correct or not it is certainly not altogether far-fetched, for ferments sometimes occur in animal and plant fluids which may not be used for digestion. Neither Vines' experiments nor those of the author up to date prove conclusively that bacteria are *not* at work in the pitchers. And as a matter of fact bacteria are normally present in the pitchers and have been isolated in the course of this work.

The constitution of the pitcher fluid requires further investigation. The following tests have been applied to that from Cephalotus pitchers:—

1. Litmus—Neutral.
2. Biuret test—No result.
3. Millon's Re-agent—No. ppt.
4. HNO_3—Slight ppt.
5. Na HO.—ppt.

The tests serve to indicate that the pitcher plant fluid contains very little protein, a rather extraordinary result considering the presence of insects in the fluid. One would have expected a marked biuret reaction.

Here again, however, the results of this Cephalotus research resemble those of Vines on Nepenthes. "The general conclusion at which I arrive is that either the enzyme is not a proteid or, if it is, it is present in extremely minute quantity, though it is difficult to accept this alternative in view of the remarkable digestive activity of the liquid." (Vines.)

The products of digestion when it occurs in vitro in the presence of acid are always characteristic, and the resultant fluid gives a marked pink biuret reaction. Such digestion is, therefore, rather like peptic digestion resulting in peptone-like products. This, how-

ever, must only be considered as tentative. It is certainly evident that up to the present the complex nature of the bio-chemistry of the pitcher plants has not been suspected. Would it be possible to account for the presence of the pitchers and the extraordinary glands secreting fluid, without reference to insect feeding?

It has already been suggested that the fluid of some pitcher plants is secreted and kept in the pitchers to be re-absorbed when required by the plant. Then, again, the secretion of water by hydathodes has been explained as of great use to plants which are living in such a moist atmosphere that little transpiration, *i.e.*, evaporation from the leaves can take place. Owing to the secretion of water by such glands a water current may be set up in the plant when it would otherwise be very feeble. Now, Cephalotus grows under conditions which are most unfavourable for transpiration. It is a low plant, sheltered from air currents and it is found on extremely moist ground. The retention of the water in the pitchers would, however, require explanation, and I think it straining the point too far to imagine that this fluid is required for reabsorption during the dry weather. The dry season is very short at Albany, and the ground, where the pitcher plants grow, never becomes very dry so far as I know. We may consider this another possible reason for the presence of the glands and the pitcher fluid, but it does not seem sufficient to account altogether for the evolution of an elaborate pitcher which usually contains insects, and seems specially fitted for their capture.

Is there any reason why our pitcher plant should require food in organic form? We have already shown that it can be cultivated without it. The fact that the pitcher plant can be grown without the provision of insect food does not form a stumbling block to a belief in its carnivorous propensities, for Busgen, in 1888, showed that Utricularia would grow without animal food, but that the provision of the latter resulted in double the development. It was demonstrated also in 1883 that Drosera could be grown apart from insects, but that plants allowed to capture and digest insects were 1½-3 times the dry weight of those not fed in this way and they produced more flowers and fruit. We hope to have a similar series of experiments set going with Cephalotus in order to discover whether there is any marked difference between plants fed with insects, etc., and those which have been kept without organic matter.

In the meantime it must be pointed out that very many of the carnivorous plants grow on somewhat boggy, peaty soils. This is particularly the case with the sundew in Great Britain and Europe and our Western Australian pitcher plant. Now, if there is some factor common to the environment of these plants which are in many ways different but agree in the physiological feature we are studying, this common factor may explain the carnivorous habit.

It is already known that there is some difficulty in obtaining Nitrogen from this peaty soil, and it has been suggested on this account that the carnivorous habit is to be associated with the procuration of an extra supply of Nitrogen in the form of organic compounds. We have, therefore, two theories, both of which will fit our pitcher plant.

Summary.

The following may be taken as a brief summary of what is known to-day of the West Australian Pitcher plant—*Cephalotus follicularis*:—

1. The pitchers capture insects, and in large quantities.
2. The capture of insects is not absolutely necessary for the growth of the plant and the formation of new parts or the development of flowers.
3. The fluid in the pitchers contains a digestive ferment which will break up proteids into peptone-like bodies in a very short time in the presence of acid.
4. It has not been shown (nor is it true for Nepenthes) that this is the mode of digestion actually taking place in the pitchers, and as a matter of fact non-acidulated pitcher fluid does not digest proteid, or, if so, very slowly in vitro.
5. It is possible that digestion in the pitchers is due to the action of the ferment and that this digestion takes place very slowly.
6. The environment of the West Australian pitcher plant suggests that the development of pitchers with glands serves two purposes—
   (a.) It provides for a water current in the plants by the secretion of water from the pitcher walls. This would be an advantage, seeing that the plants are unfavourably situated for transpiration.
   (b.) It provides another method for the obtaining of nitrogen—a necessary element procured with difficulty from peaty soils.
7. Experiments are now being arranged to determine the effects produced by feeding the pitchers with insects and different organic compounds, comparisons being made with other specimens growing without such additions.